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Abstracts From the 6th North American Echinoderm Conference

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ABSTRACTS FROM THE 6TH NORTH AMERICAN ECHINODERM CONFERENCE

Activity of *Patiriella regularis* and *Meridiastra mortenseni* in Lowered Salinity

M. F. Barker

Unique climatological and hydrographic conditions in Fiordland, southwest New Zealand, produce a near freshwater layer (LSL) on top of full-salinity water. The asteriniid starfish *Patiriella regularis* is often found within this LSL, while the closely related and morphologically similar *M. mortenseni* occurs immediately below it in full-salinity seawater. Laboratory and field experiments have shown that in the southern fiords *P. regularis* tolerates low salinities and can even survive in freshwater for several days while *M. mortenseni* is unable to live at salinities much less than 35‰. To examine whether salinity tolerances found in fiordland asteriniids are unusual, the activity of *P. regularis* and *M. mortenseni* was determined in starfish collected from sites on the west and east coast of the South Island and from the east coast of northern New Zealand and from Tasmania in Australia. Activity coefficients of sea stars bathed in salinities of 34, 26, 16, and 9‰ immediately after collection show that *P. regularis* from Doubtful Sound have higher activity in all lower salinities tested than sea stars from all other populations examined. However, in experiments in which *P. regularis* were held at a salinity of 9‰ for up to 8 hr, sea stars from the Derwent River in Tasmania generally had higher activity at each of the times tested. All populations of *P. regularis* have higher activity in diluted seawater than two populations of *M. mortenseni* tested.

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Studies of a Symbiotic Association Between Subcuticular Bacteria and Sea-Star Larvae that are Widely Distributed in the Sargasso Sea and the Gulf Stream

I. Bosch, E. St James, and W. B. Jaeckle

Clonal bipinnaria larvae comprising at least four different types have been reported at densities of more than $11 \cdot m^{-3}$ in surface plankton collections from the Gulf Stream and the Sargasso Sea in the western North Atlantic. One particular type of bipinnaria that has been provisionally assigned to the genus *Oreaster* on the basis of mt-tRNA gene sequence analyses is host to assemblages of bacteria that live beneath the cuticle in epidermal regions around the larval gut. The goal of this ongoing study is to identify the symbiotic bacteria and to determine the nature of the symbiotic association. We have found that the bacterial layer is brightly fluorescent under FITC, TRITC, and Texas Red fluorescent filter combinations even in preserved samples. Fluorescence intensity measured for whole larvae using broadband excitation in a NanoDrop ND-3300 fluorospectrometer was the equivalent of 3–55 nM concentration of FITC with peak emission wavelengths ranging from 471 to 519 nm. Work on rDNA isolation and sequencing analyses of bacteria associated with preserved larvae and from cultures isolated from freshly collected bipinnarias will continue throughout summer 2011.

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Growth in the Field in *Ophioplocus januarii* (Ophiuroidea) Using Chemical Tagging

M. I. Brogger and P. E. Penchaszadeh

A previous laboratory experiment has shown that chemical tagging using calcein may be prospective to study growth in the brittle star *Ophioplocus januarii*. Individuals marked with this chemical showed a distinct green fluorescent mark in different ossicles, with jaw marks notorious and well defined. Field growth studies were conducted using capture–mark and recapture along a 1-yr period at northern Patagonia (Argentina). A total of 720 ophiuroids were tagged with calcein, with an overall recapture of 6.9%. Two jaws of each recaptured brittle star were included in resin, sanded and polished, and observed with epifluorescence at the microscope. Growth analysis was conducted from size-increment data. Individual growth was estimated measuring jaw ossicles, between fluorescent marks (initial size) and between current borders of the structures (final size). The morphometric between body size and dental plate and teeth length follows a power functional relationship, being able to predict body size on the basis of jaw measurement observations. The growth constant K for the studied population is $0.222\ yr^{-1}$ and the infinite size L_∞ equal to 20.4 mm disc diameter. The estimated maximum age for *O. januarii* is

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18 yr. Comparisons with available growth parameters of other species are discussed as well as different methodologies used to study growth in Ophiuroidea.

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Visceral Regeneration by the Uptake of Dissolved Organic Material in the Sea Cucumber *Parastichopus californicus*

C. J. Brothers, J. R. Nestler, and R. W. Lee

Regeneration allows living organisms to repair or replace body tissues in response to sublethal predation or stressful abiotic conditions. The holothurian *Parastichopus californicus* is a unique model for studying the regenerative process as every year the visceral organs atrophy between October and November and regenerate between January and March. Previous research has suggested that during the period of regeneration no movement or feeding occurs; however, the metabolic rate is doubled when compared with the period during which regeneration does not occur. The uptake of dissolved organic material (DOM) from the aqueous environment could provide an external source of biosynthetic materials for regeneration of the visceral organs. In April, adult *P. californicus* were incubated in ^{15}N-labeled dissolved amino acids (Isogro©) for 48 hr and the uptake of ^{15}N by the epithelial (dorsal and ventral), buccal tentacles, tube feet, longitudinal muscle strips, digestive tract, gonads, Cuvierian tubules, and respiratory tree tissues was measured. Uptake by respiratory tree (δ^{15}N 223.2 ± 80.5) was significantly higher than all other tissues, and uptake by muscle (δ^{15}N 11.5 ± 0.3) was significantly lower than all other tissues. Uptake by tube feet (δ^{15}N 28.2 ± 10.7) and buccal tentacles (δ^{15}N 27.9 ± 8.6) was significantly higher than all other tissues except respiratory trees. These results suggest that certain tissues of *P. californicus* take up dissolved amino acids from the seawater that could be used as biosynthetic materials for regeneration. Ongoing studies are examining DOM uptake during these animals' most active season (July–August), atrophy phase (October–November), and regeneration phase (January–March).

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Paleoechinodermatology 101: Tertiary Echinoderms of the Pacific Northwest

C. Burns and R. Mooi

We summarize current knowledge of and research on Tertiary echinoderms from Oregon and Washington. These are found in a variety of novel preservational scenarios rarely encountered elsewhere, resulting from the Northwest's dynamic plate tectonic history. Well-preserved isocrinids represent their last stand in the northeastern Pacific, and their paleoecologic factors resulting in spectacular Lagerstätten are now well understood. Several asteroid and ophiuroid discoveries add new data to the evolution of the diverse NE Pacific fauna. Spatangoids and cidaroids are common. New data are being accumulated about the earliest protoscutellid clypeasteroids and their later descendants. This data recovery is of paramount importance due to predicted future inaccessibility of the collecting localities.

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Reduced Growth under Conditions of Near-Future Ocean Acidification in the Ecologically Important Sea Urchin *Lytechinus variegatus*

R. C. Challener and J. B. McClintock

Increasing concentrations of anthropogenic-derived atmospheric CO_2 are decreasing the pH of the world's oceans. Many marine calcifying organisms, especially echinoderms with Mg-calcite skeletons, may be influenced by near-future (end-of-century) ocean acidification. We investigated the impacts of acidifying seawater conditions (pH 7.7 vs control pH 8.1) on the juvenile to early adult phase of *Lytechinus variegatus*. Urchins were fed a formulated diet and held individually in tanks for 14 wk; pH was controlled by bubbling CO_2 and air into artificial seawater. Growth (wet weights, test diameters, and body component indices), consumption, and fecal production rates were assessed. After

14 wk, urchins exposed to reduced pH displayed significantly reduced growth (smaller test diameter and wet weight) but increased gut indices. No significant differences between pH treatments were found in consumption (g dry feed intake/g animal d^{-1}), yet urchins exposed to acidified seawater (pH 7.7) had significantly higher fecal production rates (g/g animal d^{-1}) than those in the control pH treatment. These results indicate that reduced growth in *L. variegatus* under conditions of ocean acidification is likely attributable to a reduction in the ability to process nutrients. Responsible factors could include a more rapid movement of food through the gut, reduced gut absorption efficiencies, compromised gut flora, or the allocation of nutrients to the gut rather than test growth.

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Mechanical Behavior of the Tiled and Actuating Exoskeleton of the Helmet Urchin, *Colobocentrotus atratus*

T. Chen, M. C. Boyce, and C. Ortiz

The helmet urchin *Colobocentrotus atratus*'s unusual reduction in spines form a smooth tiling of millimeter-sized, flattened polygonal protective plates. Each plate articulates with the underlying test via a ball-and-socket joint and the microstructure of each plate is a porous network of single-crystal magnesium-doped calcite with a few percent of intercalated organic. The galleried stereom of the individual plates was investigated via X-ray computed microtomography and found to possess a gradient in volume fraction with distance from the socket ranging from 90% at the ball-and-socket joint to 50% at the outer surface. The axial direction of the galleried structure radiates outwardly from the socket and terminated perpendicular to the outer surface of the plate. The galleried mesh (average pore size ~15 μm) was modeled using three-dimensional elastic finite element analysis that consisted of a microstructurally based parametric representative volume element with periodic boundary conditions. Various loading configurations were simulated to obtain anisotropic stiffness tensors and resulted in an orthotropic effective mechanical behavior with the stiffness in the plane transverse to the long axis of the galleried microstructure (E1, E2) approximately half the stiffness in the axial direction (E3). With parametric simulations, E3 was found to decrease linearly from 0.87 of the solid elastic modulus (E_s) to 0.34 of E_s as the volume fraction decreases from 0.88 to 0.46. In the transverse direction, E1 and E2 also decrease linearly from 0.49 of E_s to 0.18 of E_s within the same range of volume fraction. Spatial gradients in density were also modeled, corresponding to the gradient in porosity in the plate. This open-pore structure and trabeculae alignment results in a directional strengthening due to inhomogeneous deformations in the porous structure and provides resistance against blunt impacts and containment of penetration into the surface of the plate.

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Luidia lawrencei (Echinodermata: Asteroidea): To Be, or Not to Be, That Is the Question

M. P. Cortes, H.-M. Chung, and C. M. Pomory

Luidia clathrata was recently split into two species, *Luidia clathrata* and *Luidia lawrencei*, on the basis of morphological, isozyme, and genetic data. Individuals matching the morphology of the recently described species were compared in behavior (particle size choice) and physiology (acute salinity tolerance), as well as with analysis of genetic material. Behavior was assessed by examining choice of substrate among four grain size ranges (125–249, 250–499, 500–999, and 1,000–2,000 μm). Physiology was assessed by examining righting response in relation to acute reduction in salinity from 35 practical salinity units (psu) to lower salinities. Genetic homology was assessed using segments within the COX-I mitochondrial gene. No significant difference was found between species for sediment grain size choice. All individuals of both species righted themselves in salinities of 35, 30, and 25 psu after 30 min of exposure. At 22 psu 89% of *L. clathrata* and 56% of *L. lawrencei* individuals righted themselves. At 20 psu 32% of *L. clathrata* and 0% *L. lawrencei* individuals righted themselves. Righting time increased at salinities below 30 psu for both species. Righting time was shorter for *L. lawrencei* in 35, 30, and 25 psu and similar between species in 22 psu. Mitochondrial genome comparison returned over 99% homology among the species. Although the salinity data indicate a difference between the species, which may be an acclimation response, our genetic result, contrary to what has been previously published, does not support the recently proposed separation of the species. Other differences may be phenotypic responses.

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Formation and Growth of Vertebrae in Brittle Stars: Do Ossicles Ever Fuse?

H. M. Croce and R. L. Turner

It has long been thought that vertebral ossicles in arms of brittle stars evolved by fusion of paired ambulacral ossicles. Researchers examining the development of ophiuroids often focused on the external rather than internal features, and, due to the presence of the ventral and lateral arm plates, the development of the vertebrae has not been well studied. Here, the development of the vertebral ossicles of *Ophiophragmus filograneus* near the growing tip of the arm was examined. Arm tips, cleaned of soft tissue with bleach, were studied using scanning electron microscopy. It was found that the vertebral ossicles originate under the ocular in halves. The two ambulacral ossicles grow toward each other with much branching of the stereom, eventually interdigitating in the manner of a three-dimensional jigsaw puzzle. As the vertebrae grow, the two ambulacral ossicles interlock more tightly, creating a suture line, which has been taken before as evidence for incomplete fusion of the halves. Some evidence of fusion was found in the more mature vertebrae, in which the suture line was sometimes not visible. Further study is needed to determine conclusively whether fusion, either partial or in full, occurs between the two halves of the vertebral ossicles of ophiuroids, or if, as this study suggests, interdigitation forms an immobile joint, a gomphoid synarthrosis, between the halves. A tendency not to fuse has implications for echinoderm tissue dynamics, and other systems of ossicles in which fusion has been claimed to occur should be re-examined.

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Concurrent Growth and Differentiation of Regenerating Arms in Brittle Stars

H. M. Croce and R. L. Turner

Regeneration of body parts from sublethal predation and disturbance is common in ophiuroids. Because arms play a critical role in feeding, rapid functional recovery is critical. Some investigators suggest that the cost of arm regeneration results in a trade-off between functional recovery (differentiation) and regrowth of lost length. This study examined the hypothesis that growth and differentiation occur concurrently along a regenerating arm. Intact and regenerating arms of the ophiuroid *Ophiophragmus filograneus* were compared using scanning electron microscopy to test this hypothesis. Arms were examined with soft tissue present and with it removed by treatment with bleach. With soft tissue present, both intact and regenerating arms clearly displayed arm segments (demarcated by dorsal or ventral plates) that continuously increased in length from the arm tip (ocular or terminal ossicle) to the point of autotomy. Near the ocular, segments were difficult to distinguish with soft tissue present, but arm plates, vertebral ossicles, and sometimes the ocular were readily visible in bleached arms. Soft tissue can obscure differentiated skeletal elements toward the arm tip, but, once removed, the skeletal elements become clearly visible. This study found that growth and differentiation of the skeletal elements of regenerating arms do occur concurrently. No evidence was found of a trade-off resulting in growth without differentiation during arm regeneration.

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Righting Behavior in Intact and Autotomized Sea Stars (*Asterias forbesi*)

C. J. Demauro and P. C. Daniel

Sea stars are capable of exhibiting directionality for a number of behaviors despite being pentaradial and lacking a central nervous system. Directionality appears to involve establishment of temporary dominance by one or several arms. In righting behavior, several arms will roll and attach tube feet (planting), thus establishing their ''dominance,'' followed by somersaulting of the remaining arms over the central disc. Sea stars are well known for their ability to voluntarily lose arms (autotomy). Righting behavior in *Asterias forbesi* was filmed and analyzed using three-dimensional kinematics in intact sea stars (n = 20) and then following autotomy of one arm (n = 20) and two arms (n = 10). Autotomy resulted in a significant decrease in righting time. Because there are fewer arms available to plant in autotomized individuals there are fewer combinations of outcomes available. If there is a ''competition'' between arms then this should lead to a decrease in the time it takes to establish the planted arms. In intact animals any arms might be used in planting in a given trial. There was no significant preference in direction of righting. Following either single or double autotomy, sea stars avoided planting arms adjacent to an autotomized arm and showed a clear preference toward righting in a direction opposite the autotomized arm or arms. Direction of righting could be predicted by the positions of the two lowest rays at the beginning of the righting trial for both intact and autotomy treatments. Autotomy appears to cause a consistent imbalance in the

animal. Thus arms closest to the surface are most likely to make first contact, which in most cases results in them becoming the planted arms and establishing dominance. Coordination between radial nerves in the arms seems to be a necessary component to successful righting behavior.

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Fluid Dynamical Analysis of Recent and Fossil Crinoid Suspension-Feeding Mechanisms

J. F. Dynowski, J. H. Nebelsick, and A. Roth-Nebelsick

The long and complete fossil record of crinoids enables detailed morphological comparison with their living representatives. In the past, stalked forms were very abundant and, in contrast to today, were living predominantly in shallow-water habitats. Current regimes in shallow water have more rapidly changing current directions and velocities than in deep-sea habitats. Recent stalked crinoids possess highly flexible feeding structures allowing for a typical filtering position with the arms bent backward into the current. Alternative feeding positions thus have to be assumed for some fossil crinoids that did not possess such a high flexibility. The presented ongoing study investigates (1) general suspension-feeding mechanisms of crinoids; (2) different feeding positions and their effect on flow patterns; and (3) different filter architectures and their effect on filter efficiency. For this study, the fossil crinoid *Encrinus liliiformis* from the middle Triassic Muschelkalk (243–235 million years) of Central Europe and the recent *Hyocrinus* sp. are analyzed. To gain insights into the circulation pattern around both crinoids, two methods are applied: (1) particle image velocimetry measurements in a flow tank using resin models; and (2) computational fluid dynamics simulations of three-dimensional models using the software CFX ANSYS Academic Research Release 12.1. First results show that the application of both methods creates similar results. For *Encrinus*, the analyses reveal that a backward current is generated, allowing for food particles to be directed back into the crown. By opening the arms or pinnules the current patterns vary, indicating possible reactions of the animal to changing flow conditions. Further analyzes are needed for the comparison to the recent *Hyocrinus*.

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Reproductive Changes of *Strongylocentrotus purpuratus* Along the North American Coast: Ocean Conditions and Bottom-Up Modifications

T. A. Ebert, J. C. Hernández, and M. P. Russell

Gonad production of the purple sea urchin, *Strongylocentrotus purpuratus*, was studied during 2007–2009 at sites from Vancouver Island, British Columbia, Canada, to Punta Baja, Baja California Norte, Mexico, and related to the multidimensional ENSO index (MEI), which influences algal production and hence gonad development. No latitudinal patterns were detected, although there were differences across sites. For northern sites, gonad data from 2007 to 2009 were negatively correlated with the MEI with a lag of 9 to 11 mo and positively correlated with a lag of 2 to 4 mo. Southern sites were more variable. Historical gonad data from Yankee Point, CA from 1952 to 1964 showed a negative correlation with the MEI. The period from 2007 to 2009 had negative MEI values and historical dissections during the mid-1960s into the early 2000s, when the MEI was more positive, all tended to show lower gonad production.

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Ed Ricketts, Walter Fisher, and a Forgotten Account of the Sea of Cortez Sea Stars

D. J. Eernisse

Ed Ricketts was a dedicated hard-working zoologist and devoted father; he shrugged off the beer-drinking, womanizing ''Doc'' image portrayed by his best friend, John Steinbeck's novel *Cannery Row*. He also somehow managed to not hold a grudge when the world's foremost sea-star authority, Professor Walter Fisher, who was then the Director of Hopkins Marine Station just down the street, wrote a condescending review of Ricketts' first 1931 submission (with Jack Calvin) of the manuscript for *Between Pacific Tides*. It was finally published in 1939 and is now recognized as a highly readable account of West Coast marine invertebrates and a landmark in ecology. Fisher had criticized the book's organization by habitat not by taxon, and implied that Ricketts was merely a collector, not a

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professional zoologist. After its publication in 1939, and Steinbeck's *Grapes of Wrath* published that same year, the best friends hatched a plan for a biological expedition to the Sea of Cortez, with a coauthored book to follow. Under Ricketts' direction, the small group managed to visit 18 localities over a 25-d period, carefully preserving thousands of representative marine invertebrates for later study. Although the adventure is better known, the work that followed is even more impressive. Ricketts returned and prepared a detailed scientific appendix for the book in less than a year, integrating his field observations with extensive library research and identifications by the best available taxonomic expertise. The sea stars featured prominently. Fisher gave Ricketts complete access to his personal library and contributed identifications, and local artist Alberté Spratt provided stunning illustrations. All but one of the then-known Gulf shallow-water sea-star species were collected and described. Sadly, Pearl Harbor was bombed within days of publication of *Sea of Cortez*, the book went out of print, and this integrative natural history gem has been seldom cited.

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Analyzing Intraspecific Variations of Jurassic Echinoids

J.-P. Friedrich and J. H. Nebelsick

The main focus of this study deals with the assembling of a basic data set concerning the morphological variation of various Jurassic echinoids using three-dimensional morphometric analyses. Until now, most studies on morphometric variations have examined Recent irregular echinoids, in which the data were collected by two-dimensional photometrical analyses. A two-dimensional morphological examination is only possible with the flattened irregular echinoids. Regular echinoids, however, due to their more rounded shape, need a three-dimensional approach and interpretation to capture their morphological features. The bases of the present analyses are the well-preserved Jurassic echinoids in the collections of the Institute of Geosciences, Tübingen and the State Museum of Natural History in Stuttgart, Germany. Especially the common regular echinoids of the genera *Plegiocidaris* POMMEL, which are present in large numbers and are generally well preserved, constitute the focus of this investigation. In addition, a further cidaroid *Paracidaris* POMMEL as well as the irregular echniods *Nucleolites* LAMARCK and *Galerites* LAMARCK are investigated. The individual echinoids are scanned three dimensional by µCT and optical scanners, and interpreted by landmark analyses. Expected results of these morphometric studies include information on: (A) variations within populations. This includes the natural variations between adult individuals of a species, variations within the ontogenetic stages, and possible variations due to sexual dimorphisms; (B) variations of morphology through time to discern evolutionary trajectories in morphology through time.

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Resolving Conflict Between Molecular and Morphological Evidence for Neoasteroid Phylogeny

A. Gale

The phylogeny of neoasteroids (post-Paleozoic asteroids) has recently been the subject of three independent, extensive studies on the basis of diverse molecular data (Mah & Foltz 2011, *Zoological Journal of the Linnean Society*, 161, 769–788; Janies et al. 2011, *Systematic Biology*, DOI:10.1093/sysbio/syr044) and morphological analysis of the skeleton (Gale 2011, *Special Papers in Palaeontology* no 85). Each study has generated trees with strikingly different topologies, none of which supports traditional ideas of asteroid evolution and classification. The only consensual conclusions of these three papers are that both the Forcipulatida and Paxillosida are monophyletic and that the Asterinidae and Solasteridae are sister taxa. Major conflicts are: (1) the identification of the basal neoasteroid group; (2) the position of Velatida (Pterasteridae etc.) as either sister taxon to Forcipulatida (Mah & Foltz), basal asteroid group (Janies et al.), or highly derived Spinulosida (Gale); (3) the polyphyletic Valvatida proposed by Mah & Foltz, with complex features supposedly evolving repeatedly. Resolution can perhaps be achieved by complementary morphological, molecular, and developmental study of key taxa, extending both the range of genes and structures investigated. Additionally, the fossil record of the neoasteroids is poorly understood, but critically important in resolving phylogeny.

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Broadening your "Broader Impacts": A Proposal to the Echinoderm Research Community

J. Hodin, P. Miller, and D. Epel

Echinoderms harbor tremendous potential for enhancing biology education. Their easy-to-obtain, optically clear eggs, synchronously and rapidly developing embryos, striking larval forms, complex life cycles, deuterostome classification, unique morphologies and body symmetry, regenerative capacities, sequenced genomes, and excellent fossil record all contribute to their attractiveness for use in the high-school and university classroom. Our lab group at Hopkins Marine Station has been working for years to facilitate educational outreach using the sea urchin, most recently via two National Science Foundation (NSF)-funded websites. Sea Urchin Embryology (http://www.stanford.edu/group/Urchin/index.html), receiving millions of hits annually, was launched in 1997 primarily as a resource for teachers, offering laboratory support and class activities, and to help students initiate research projects. Our Virtual Urchin site (http://virtualurchin.stanford.edu), launched in 2006, complements the original site, offering interactive activities and tutorials ranging from teaching microscopy skills to undertaking and analyzing an ocean acidification experiment. We are especially excited about the latter: students collect and analyze real data on a current research issue by entering our ''virtual lab bench,'' setting up an ocean acidification experiment (using real data collected by our colleagues Thorndyke and Dupont), and measuring the effects on urchin larval growth. We designed this virtual lab bench in a modular fashion, and are modifying it for a lab involving embryo manipulations and microinjection. This modular design allows us to promote a wide range of research on echinoderms for effective educational outreach, now a strict requirement of many funding agencies, notably NSF. We propose Virtual Urchin's use by the echinoderm research community as a community-wide educational outreach tool, where our media design and curriculum development staff works with echinodermologists to develop high-quality educational outreach activities based upon their research. We discuss several possibilities of funding the development of these activities, including inclusion in individual research grant proposals.

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Observations on *Onychaster* Meek & Worthen, 1868 (Ophiuroidea: Onychasteridae) (Famennian–Visean age)

F. H. C. Hotchkiss and A. Glass

Onychaster flexilis Meek & Worthen, 1868, lived epizoically on the crowns of stalked crinoids and bent its arms ventrally into coils that grasped its host. Spencer (1927) saw *Onychaster* as being in the direct line of ancestry to the Recent Euryalae, with the lineage having retained its epizoic habits since the Carboniferous period. If *Onychaster* is a euryalid, then it is the first and oldest record of this crown group. THE QUESTION: Is the genus *Onychaster* properly classified as a Paleozoic representative of the extant order Euryalida (cf. Spencer & Wright 1966)? …or is it merely homeomorphic with extant euryalids (cf. Fedotov 1926)? FINDINGS: In *Onychaster* the lateral/adambulacral plates are strictly on the undersurface of the arm where they form a double row and nearly touch midventrally; there are no mid-ventral underarm plates. The undersurface laterals bear a transverse row of spines that point proximally (in retrodirection). The disk in large specimens bulges interradially such that the arms insert subambitally. The morphology of *Onychaster* vertebrae is documented anew in scanning electron microscopy stereopair images. Distinctive features include: a median dorsal cleft or circular pit on the upper surface; an auluroid canal; paired epanapophyses; a zygosphene dorsal to the auluroid canal; exceptionally spacious fossae for the ventral longitudinal muscles; and an undersurface plastron that is dimensioned like a waist belt. These features are transformationally close to eospondylid/furcasterid vertebrae and progressively/increasingly distant from zygospondylous, transpondylous, and streptospondylous vertebrae. Classification of *Onychaster* as a euryalid is not supported. We reclassify the Onychasteridae next to the Furcasteridae. The oldest occurrence of streptospondylous vertebrae, after eliminating *Onychaster*, is in the Triassic *Aspiduriella streichani* Kutscher, 1987, which is not a euryalid. The oldest/first occurrence of the order Euryalina is *Asteronyx* in the Late Cretaceous.

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An Arm-Stump Specimen of *Archaster angulatus* Müller & Troschel, 1842 (Echinodermata: Asteroidea)

F. H. C. Hotchkiss and J. K. Keesing

Specimen USNM 1139740, dry, of *Archaster angulatus*, from near Fremantle, Western Australia, has an arm stump that healed and did not regenerate the arm tip. DESCRIPTION: The stump is 26 mm long, 14 mm wide; the intact

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rays measure $R = 65$ mm, 13 mm wide. The stump furrow is 19 mm long with 14 tube feet; no terminal tentacle; the radial nerve is visible. Well-formed; not a recent event. The distal adambulacral, inferomarginal, and superomarginal plates of the two sides arc and join smoothly to form the rounded terminus; no terminal plate. The distal four inferomarginals of the hairpin turn correspond with only three superomarginals: the 9th superomarginal of the left side is enlarged and imprecisely overlies the 9th and 10th inferomarginals. The superomarginal at the tip of the arm stump overlies imprecisely/partially the most distal (10th) inferomarginals of each side of the arm. FINDINGS: The structural organization seen in this arm stump, together with its failure to regenerate, has been described before in a *Linckia laevigata* and an *Asterias rubens*, and their previous analysis still holds (Hotchkiss 2009). *Archaster* and *Linckia* belong to separate families within the order Valvatida and *Asterias* belongs to the order Forcipulatida. Recurrence of this stump condition in taxonomically distant species indicates that pattern regulation is involved. Analysis based on positional information theory and regeneration models indicates that positional information in the starfish arm is symmetrical, and that the best-fit model for starfish arm regeneration is the *distalization followed by intercalation model* (Agata et al. 2003, 2007). This finding postulates that distal outgrowth of the starfish arm in both intact and regenerating specimens is by intercalation between a distal signaling center and the last-formed section of arm. This description compares favorably with the observed location of addition of new plates just proximal to the terminal plate.

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The Paleoecology of a New Hydrocarbon Seep Mound-Dwelling Sea Lily (Crinoidea, Echinodermata) from the Upper Cretaceous (Campanian) Tepee Buttes, South Dakota, United States

A. W. Hunter, N. Landman, N. Larson, and T. Oji

Despite a rich and varied record, post-Paleozoic stalked crinoids are relatively rare in the Western Interior Seaway of North America compared with those found in northern Europe. In this study we describe a unique example of post-Paleozoic crinoid from the Tepee Buttes, preserved within the remains of cold methane seeps (hydrocarbon seep mounds), from the Upper Cretaceous (Upper Campanian) of the northern Great Plains of the United States. This northern part of the Cretaceous Western Interior Seaway has never before yielded any identifiable crinoid remains. Nevertheless there have been significant studies on crinoids in other parts of the Upper Cretaceous of North America that have provided a good basis for study. We propose that the erection of a new order is required, as no existing order within the Articulata can accommodate all the characteristics of this new genus. We have found that this crinoid shares many features with other members of the articulates, including bourgueticrinids; however, it is apparent that this taxon is most closely related to the bathycrinids. Reconstructing the entire crinoid using over 50 semiarticulated and disarticulated (well-preserved) fossils, we reveal a unique paleoecology and functional morphology specifically adapted to living within this hydrocarbon seep environment. Finally, we will discuss how the morphology of this relatively shallow-water taxon relates to its deepwater, living, and fossil cousins the bathycrinids.

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The Anus as a Second Mouth: Anal Suspension Feeding by an Oral Deposit-Feeding Sea Cucumber

W. B. Jaeckle and R. R. Strathmann

Respiratory trees of holothurians are blind-ended evaginations of the posterior digestive system that are rhythmically inflated with seawater via the anus and are considered to have respiratory and excretory functions. We tested the assimilatory capability of the respiratory tree epithelium by exposing adults of the oral deposit-feeding aspidochorotid sea cucumber *Parastichopus californicus* to (1) ^{14}C-labeled unicellular algae and (2) iron-containing macromolecules and then following the distribution of the label in tissues. The ^{14}C label distribution indicated uptake by the respiratory tree and transfer to the associated hemal system. The iron label from the protein ferritin

and the polysaccharide iron dextran entered cells of the endothelium; mesenchyme cells within the connective tissue compartment of the respiratory tree were labeled in ferritin-exposed trees, suggesting an avenue for transfer of materials. Nutritionally, holothurians appear to be bipolar anal retentives; the anus serves as a second mouth.

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Salinity Effects on Arm Regeneration in *Luidia clathrata* (Echinodermata: Asteroidea)

K. E. Kaack and C. M. Pomory

The effect of salinity [20 practical salinity units (psu), 25 psu, and 30 psu] on regeneration of two arms of the starfish *Luidia clathrata* was examined in a laboratory experiment to test the hypothesis that regeneration in *L. clathrata* is adapted to euryhaline conditions found in bays. On the basis of univariate and multivariate analysis, regenerating arm condition relative to treatment was 20-psu treatment < 25-psu treatment < 30-psu treatment, and nonregenerating arm condition was 20-psu treatment < 25-psu treatment = 30-psu treatment. Arm regeneration in *L. clathrata* is not well adapted to lower salinity conditions, despite common occurrence of the species in bays. Lower salinity in bays should reduce ability of *L. clathrata* to recover from damage sustained during, or just prior to, low-salinity periods.

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Fossil Brittle Stars from the Paratethys (Miocene, Europe)—State of the Art

A. Kroh and B. Thuy

The Paratethys was a large sea that formed during the Eocene and was separated from the Mediterranean by the rise of the alpidic mountain chains. This shallow epicontinental sea is one of the best-investigated fossil basins. Being easily accessible in abundant artificial and natural outcrops, its deposits were intensely studied by 19th- and 20th-century paleontologists. Yet some taxonomic groups received considerably less attention than others. Brittle stars that are common in equivalent modern settings were largely ignored so far. In part this may be explained by their multielement skeleton that tends to fall apart rapidly after death. Here we present the current state of knowledge on Cenozoic brittle-star assemblages of the Paratethys. Articulated specimens are exceedingly rare; only few localities have delivered whole individuals. In most cases these specimens are embedded in silt and clay and appear to have been killed by obrution. Isolated ossicles are much more common, but tend to be restricted to a specific time slice during the Middle Miocene. In this interval tropical conditions prevailed, providing for abundant and diverse habitats ranging from soft bottoms to coral reefs. A survey of the ophiuroid species described from these deposits shows that most are in serious need of taxonomic reassessment, often being placed indiscriminately in a few genera (mostly *Amphiura* and *Ophiura*). Detailed analysis of topotypic material, however, shows a rich diversity similar to analogous modern environments (e.g., the Caribbean).

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Factors Influencing the Distribution and Population of the Grazing Urchin *Echinometra mathaei* within the Ningaloo Marine Park

M. W. Langdon, M. van Keulen, and E. I. Paling

Sea urchins can have a significant influence upon the ecological structure of coral reefs through bioerosion of substrata and also by affecting competition for space. They are important grazers in many marine systems and can cause major ecosystem changes when their populations reach high levels (generally after a decline in the numbers of their fish predators). However, the relative importance of the role of sea urchins in influencing the composition and structure of coral reef habitats has rarely been explored. This study is linked to the CSIRO Wealth from Oceans Ningaloo Collaboration Cluster, Component 1: Habitat Mapping and Biodiversity. It has so far examined coral reef habitats and macroinvertebrate (particularly urchins) distribution and abundance within Ningaloo Marine Park. Field sampling has been undertaken at over 100 sites within the park, focusing on nearshore,

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lagoonal, and back reef areas within sanctuary zones and adjacent recreation zones. Data analyses so far indicate that the distribution of urchins is not affected by the management zones of the park (i.e., no significant evidence has been found of indirect effects from fishing of urchin predators). However, habitat type has a major influence on urchin distribution, e.g., urchin populations were higher on nearshore intertidal and subtidal reef platforms, lagoonal patch reefs, and shallow backreef platforms than other habitats. In coral reefs in other parts of the world, unusually high urchin populations can indicate overfishing. So far, this study has found no indication of fishing pressure indirectly affecting urchin densities, which suggests that the current zoning may be effective. However, further analyses of the data, particularly those from the nearshore sanctuary areas where shore-based fishing activities are allowed, are yet to be completed. If fishing pressure is having an effect, it is likely to be seen in those areas where urchin abundance is predicted to be highest.

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Symmetry of the Rays of *Luidia clathrata* (Echinodermata: Asteroidea)

J. M. Lawrence, C. M. Pomory, and G. Trowbridge

We know of no documentation of the degree of symmetry of the rays of asteroids. We tested the hypothesis that rays of *Luidia clathrata* are symmetrical. We collected *L. clathrata* from Old Tampa Bay. After they were dried, the length of rays of 111 individuals with five flat, noncurved and nonregenerating rays was measured in triplicate with electronic calipers to the nearest 0.01 mm. The position of each ray in relation to the madreporite was designated by Carpenter's system. Paired t-tests on all pairs of rays were used to test for the degree of variation in ray length. The maximum difference in ray lengths of an individual ranged from 0.5 to 11 mm (SE of mean ray length per individual ranged from 0.9 to 2.4 mm). This indicates tight control of length of a ray. However, pairs of individual rays varied in length. Ray pair B and E was shortest. Ray pair C and D was longest. Ray A was intermediate in length. Ray pairs on the same side of the bilateral plane established by the madreporite, ray pair B and C and ray pair D and E, were significantly different in length. Pairs of rays diagonally across the bilateral plane, ray pair C and E and ray pair B and D, were significantly different in length. This indicates that the *L. clathrata* measured were bilaterally symmetrical in relation to the position of the madreporite and only superficially radially symmetrical. Length of the ray had no effect on bilateral symmetry. The mechanism for the difference in ray length is not known. The small difference in ray length is unlikely to have a functional effect.

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Morphological Comparison and Gametic Compatibility Among Color Morphs of *Paracentrotus gaimardi* (Echinodermata: Echinoidea)

E. M. Lopes and C. R. R. Ventura

Five color morphs of *Paracentrotus gaimardi* can be distinguished on the coast of Rio de Janeiro: black, brown, gray, green, and pink, all living in sympatry and apparently under the same selective pressures. This study compares these color morphs morphologically and investigates the existence of gametic compatibility among them. All features reported in the original diagnosis were found in all specimens of all morphs. The number of lateral spines on globiferous, a small type of ophicephalous, and the pattern of pedicellaria distribution on test are reliable morphological features to taxonomy. In contrast, the number of tubercles on genital plates varies according to growth. Despite the variation in color and number of spines in globiferous pedicellaria, the five morphs do not show clear morphological differentiation. Regarding gametic compatibility, no cross was completely unsuccessful. The successful fertilization rate was equal to or higher than 79%, and all control crosses achieved nearly 100% of fertilization. However, asymmetric gamete incompatibility was found between some color morphs. The pink morph was the most incompatible among them, with percentages of successful fertilization significantly lower in both directions. The fertilization barriers among these five sympatric color morphs are not completely evident, and these imperfect barriers to gene flow are also reflected on genetic divergences previously found in bindin and ATPase genes. However, selective process should be occurring to favor fertilization between the same morphs. Further information about spawning timing of morphs, sperm competition, and fitness of hybrids are the next steps to provide a more comprehensive view about the maintenance of these color morphs in sympatry.

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Association of a Fish Parasite, *Uronema marinum*, with the Sea Star *Leptasterias* spp.

T. J. Loveday, J. R. Nestler, and H. J. Small

Sea stars of the families Asteriidae and Asterinidae are associated with a variety of parasites including the facultative, histophagic ciliate *Orchitophrya stellarum*. In male sea stars *O. stellarum* feeds on the testes and spermatozoa, whereas in females it resides on the aboral surface as a commensal. Sea stars of the genus *Leptasterias* collected near Anacortes, WA showed pathological signs that are typical of infections with *O. stellarum*, such as reduced and discolored testes. The ciliate infecting *Leptasterias* spp. testis tissue was cultured and identified through morphological characteristics as *O. stellarum*. However, genetic analysis of the ITS1–5.8S–ITS2 ribosomal region identified the ciliate as a strain of *Uronema marinum*. *Uronema marinum* is a facultative parasite in the same subclass, Scuticociliatia, as *O. stellarum*. Typically *U. marinum* is found infecting the tissues of various marine fish and until now has not been documented as infecting sea stars.

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New Sclerodactylidae Fauna (Holothuroidea) from the Argentine Sea

M. I. Martinez and P. E. Penchaszadeh

There are 27 species of Holothuroidea reported from Argentina. These species are included in three orders: Apodida, Molpadiida, and Dendrochirotida. The latter includes three families: Psolidae, Cucumariidae, and Phyllophoridae, with no register, until now, of Sclerodactylidae. The present work identifies two new species from the family Sclerodactylidae, with distribution in the Argentine Sea. Surrounding the esophagus is a ring of large calcareous plates (the calcareous ring), which forms a support for the esophagus and is a point of insertion for different muscles. This structure has projections in Sclerodactylids and is entire for the ring pieces and divided in few pieces for the projections. Both new species have different podia distribution, representative of two subfamilies. One species is a member of the subfamily Sclerodactylinae, with podia all over the body, and the other is a Sclerothyoninae, with podia only on the ambulacra. This is the first report on the family Sclerodactylidae in the southwestern Atlantic.

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A New Genus and New Species of Sclerodactylidae (Holothuroidea) from the South Atlantic Coast

L. Martins, C. Souto, and C. Menegola

Sclerodactylidae gen. nov. belongs to the subfamily Sclerothyoninae by presenting 10 dendritic tentacles, ventral pair smaller; a compact calcareous ring with posterior processes; and radial and interradial plates uniting only at base. Its diagnostic features are the presence of tube feet scattered throughout the body, a compact calcareous ring with undivided posterior processes, and the presence of tables and rosettes in the introvert. Sclerodactylidae sp. nov. was described on the basis of 53 specimens collected in the intertidal zone from Salvador-BA, Brazil. Body oval and slightly U-shaped, numerous podia scattered. Compact calcareous ring with radial and interradial plates uniting only at the base. Radials with posterior paired processes composed of a compact piece, and a strongly concave anterior notch. Interradials spear-shaped, pointing upward. Body wall tables with oval disc, thick and knobbed margins, 2 central and 12–30 peripheral perforations, and low spire of two pillars tapering to end in 22 short rounded teeth. Introvert with tables and rosettes. Anus with tables and two-layered plates with oval perforations; tentacles with rods; and tube feet with end plate and supporting rods composed of two short spires, tapering to end in 16 small teeth. One Polian vesicle. Five groups of three papillae around the anus; under these, five anal teeth, each forming a triangle pointing outward. Color in life: most are white, brown, or gray, with dark spots scattered around the body; tentacles dark brown. Occur under rocks, inside crevices, or buried with tentacles extended toward the surface. Sclerodactylidae sp. nov. differs from the other South Atlantic Sclerodactylid,

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Euthyonidiella dentata (Cladolabinae) and *Pseudothyone belli* (Sclerodactylinae), by having 10 tentacles (vs 20), and tables, rosettes, and supporting rods (vs only plates), respectively. It differs from the other two Sclerothyoninae genera, *Sclerothyone* and *Temparena*, mostly by possessing tube feet throughout the body and tables in the introvert.

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Cellular and Molecular Mechanisms of Central Nervous System Regeneration in Sea Cucumbers

V. S. Mashanov, O. R. Zueva, and J. E. Garcia-Arraras

Echinoderms are well known for their extraordinary regenerative capacities, which include the ability to fully recover from injuries to the nervous system. Studies of the mechanisms of this rapid and complete neural regeneration will contribute to our knowledge of the evolution of neural plasticity and better understanding of neurogenesis phenomena in higher taxa. Using holothurians as an experimental model, we have demonstrated that the echinoderm nervous system possesses a major nonneural cell type that shows typical characteristics of radial glia. This cell type plays a key role in the posttraumatic neural regeneration. Transection of the radial nerve cords triggers dedifferentiation of the radial glial cells in the vicinity of the wound. The dedifferentiating cells lose their characteristic long basal processes, but remain connected to each other by intercellular junctions and form tubular outgrowths on either side of the wound. These glial scaffolds grow toward each other and are thought to support neuronal migration and regrowth of nerve processes. This growth phase is accompanied by a 10-fold burst in glial cell division in the vicinity of the wound, whereas proliferation of nonglial cells remains low. At least some glial cells of the regenerate are capable of giving rise to neurons. To understand the molecular mechanisms underlying neural recovery in echinoderms, we employ 454 pyrosequencing and in situ hybridization to characterize transcriptomic changes associated with regeneration. The response to the injury involves remarkable changes in gene expression, including overexpression of *Wnt9* and *TCTP*, which are known to be involved in patterning of the neural ectoderm and protection of cells against stress conditions and apoptosis, respectively. Moreover, among the most significantly up-regulated transcripts are retrotransposon-like elements, which are highly expressed at the wound site shortly after transection, as well as by the glial cells of the growing tubular regenerates.

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The Mg-Calcite Composition of Antarctic Echinoderms: Important Implications for Predicting the Impacts of Ocean Acidification

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The Southern Ocean is considered to be the canary in the coal mine with respect to the first impacts of ocean acidification (OA). This vulnerability is due to naturally low carbonate ion concentrations that result from the effect of low temperature on acid–base dissociation coefficients, the high solubility of CO_2 at low temperature, and ocean mixing. As such, both calcium carbonate polymorphs—aragonite and calcite—are expected to become undersaturated in the Southern Ocean within 50 and 100 yr or less, respectively. Marine invertebrates such as echinoderms, whose skeletons are comprised of high magnesium carbonate (>4% mol $MgCO_3$), are even more vulnerable to OA than organisms whose skeletons are comprised primarily of aragonite or calcite, both with respect to increased susceptibility to skeletal dissolution and being further challenged in their production of skeletal elements. Currently, despite their critical importance to predicting the impacts of OA, there is almost no information on the Mg-calcite composition of Antarctic echinoderms, a group known to be a major contributor to the global marine carbon cycle. Here we report the Mg-calcite compositions of 26 species of Antarctic echinoderms representing four classes. As seen in tropical and temperate echinoderms, Mg-calcite levels varied with taxonomic class, with sea stars generally having the highest levels. When combined with published data for echinoderms from primarily temperate and tropical latitudes, our findings support the hypothesis that Mg-calcite level varies inversely with latitude. Sea stars and brittle stars, key players in Antarctic benthic communities, are likely to be the first echinoderms to be challenged by near-term OA.

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Axes of Evol: Really Just a Big Hox

R. Mooi

Recent advances in echinoderm evo-devo include genomic sequence for an echinoid (actually now more of a reagent known as *Strongylocentrotus*). Turns out that the echinoid Hox cluster is disordered. Instead of following the usual and reasonably well-known principals of collinearity for these special regulatory genes, Hox genes of the anterior class are translocated in reverse order to the ''posterior'' end of the Hox cluster. This is not a capricious move on the part of evolution. Instead, it seems to be a method by which to arrive at the peculiar symmetry changes that occur during the ontogeny of echinoderms. These peculiarities will be reviewed and merged with what we know about homologies based on embryological and anatomical criteria in all echinoderms. This gets us closer to comprehension of echinoderms in a single framework—a sort of ''Echinoderm Theory of Everything''. Disorder of the Hox cluster does NOT mean incomprehensible disarray. It represents innovations allowing dominant adult expression of the most anterior domain (axial) over the posterior (extraxial). Hox ''disorder'' is therefore a necessary and very early echinoderm invention that superimposes radial symmetry on the anterior–posterior axis.

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Tic Tacs from the Eocene of the Pacific Northwest—Significant Clypeasteroids from Unexpected Places

R. Mooi and C. Burns

Recent discovery of specimens of the sand dollar relative, *Fibulariella*, from the middle Eocene Crescent Formation (50 ma) at Tongue Point, Clallam County, WA, represents the first northeastern Pacific occurrence of this genus. These extremely miniaturized laganine clypeasteroids (<5 mm test length) are found serendipitously in sediments lodged in crevices between basalt pillows and breccia associated with what appear to be black sand beach deposits. Other fauna in these deposits include warm-water corals, bryozoans, mollusks, brachiopods, and at least three other species of echinoids. The geographically closest Eocene relative of this likely new *Fibulariella* species is a Gulf of Mexico form presently but incorrectly known as a *Fibularia*, *F. texana*. *Fibulariella* is only now emerging as a taxon significantly different from *Fibularia* in many respects. The two genera are superficially similar due to their small size and apparent pedomorphosis, but differ greatly in overall plate architecture, basicoronal arrangement, petaloid shape, and details involving the apical system. The discovery of this new *Fibulariella* from the northeastern Pacific sheds new light on the origins, affinities, and distribution of these very early clypeasteroids.

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Unexpected Deep-Sea Echinoderm Diversity in the Early Pleistocene of the Mediterranean: Short-Term Extinction or Lack of Sampling?

L. D. Numberger-Thuy, B. Thuy, A. W. Hunter, and M. Kutscher

The Mediterranean echinoderm fauna as it is presently known is characterized by a relatively low diversity and a high abundance of eurybathic species. Typical deep-sea groups (e.g., stalked crinoids) seem to be completely absent. Here, we report on an echinoderm assemblage preserved as disarticulated skeletal elements from the early Pleistocene of Sicily, Italy. The strata yielding the echinoderm remains are interpreted as upper bathyal deposits with a mixture of shallow-water debris. The Pleistocene assemblage includes groups that are not known from the present-day Mediterranean Sea, among which are the brittle-star genus *Ophiomusium* and the stalked sea lilies *Diplocrinus (Annacrinus)* sp. and *Democrinus* sp. In addition, the assemblage documents a high diversity of ophiacanthid brittle stars, whereas the present-day Mediterranean fauna includes only two species of this deep-sea group. Remarkably, the components of this early Pleistocene assemblage are not known from the present-day Mediterranean Sea and thus exclusively consist of typical deep-sea groups. The discrepancy between the Pleistocene and the recent faunas might document selective, short-term extinction of deep-sea groups, possibly due to repeated oxygen depletion of deeper-water masses during Sapropel events or an increase in deepwater oligotrophy. An alternative scenario might be a mere lack of sampling from these deepwater settings, in which case the present study would have the potential to predict the number of typical deep-sea echinoderms to be discovered among future unbiased dredging expeditions.

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Morphometric and Meristic Changes in the Pedicellariae of the Snake Star *Asteroporpa annulata*

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Pedicellariae, the small grasping organs long known to occur on sea stars and sea urchins, have only recently been discovered in basket stars and snake stars of the family Gorgonocephalidae. The simple-armed gorgonocephalid *Asteroporpa annulata* is representative of the snake stars with the pedicellarial feeding morphology consisting of base plates, tubercles, and valves. This study examined how pedicellarial structures change along the length of the arm in the snake star *A. annulata*. The widths and numbers of base plates, the widths of, number of, and distance between tubercles, and length of valves were measured along arms of this species. Numbers and widths of base plates in segments increased with age from the arm tip to its base. Variation in width of base plates was greatest in the middle of the arm and probably indicates the intercalary addition of pedicellariae during arm growth. There was no trend in the widths of tubercles (which acted as a proxy for valve size) along the length of the arm, but their number per segment increased with segment age. Average distance between tubercles slightly increased from the arm tip to its base. Valve length was constant from arm tip to base and reflected the findings from the tubercle widths. A lack of change in valve length might indicate that there is no change in prey size captured along the length of the arm. Addition of base plates (and accompanying tubercles and valves) might provide increasingly greater prey-capture ability along the arms from tip to base in this snake star, but the arm tip with the fewest number of tubercles and base plates is still the primary site of prey capture. Although the small width of the arm tip cannot accommodate many pedicellariae, the increased flexibility of the arm at the tip and the ease of transferring food to the mouth from the arm tips probably make distal segments of the arm critical to prey capture and handling.

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Walter K. Fisher: Sea Star Expert and Courtly Curmudgeon

D. L. Pawson and D. J. Pawson

Walter Kenrick Fisher (1878–1953) was the world's leading authority on sea stars. His 51 papers on sea stars included 85 new genera and 412 new species. He laid the foundation for the modern classification of the Asteroidea. Other marine groups caught his eye. He published a monograph of Hawaiian sea cucumbers (1907), and two papers on northeastern Pacific hydrocorals (1931, 1938). Then, at age 49, he took up the sipunculans and echiuroids, describing 16 new genera and 26 new species in 10 publications. Fieldwork included two cruises on the steamer *Albatross*, to Hawaii in 1902, and from San Francisco to San Diego in 1904, and an expedition to Barbados and Antigua in 1917 with C. C. Nutting. Before he became a marine biologist, Fisher was a prominent ornithologist. He published 43 papers on birds, described two new genera, and for 3 yr edited the journal *The Condor*. Fisher graduated from Stanford University, and spent his entire career there; he was a very successful Director of Stanford's Hopkins Marine Station from 1917 until his retirement in1943. A respected voice in West Coast marine biology, he became involved in the lives of notable colleagues—Ed Ricketts, Charles Gilbert, and others. Fisher's extensive correspondence with colleagues in echinoderm research reveals him as very outspoken but well mannered. He was a close friend of A. H. and H. L. Clark, Mortensen, Deichmann, and others. A talented artist and caricaturist, Fisher illustrated his own publications, as well as the historical books written by his wife. Superb portraits painted by Fisher in his later years are highly prized today.

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A Tale of Two Brittle Stars: A Comparison of the Effects of Decreased pH and Increased Temperature on the Respiration Rates of *Hemipholis elongata* and *Ophiophragmus wurdemani* (Echinodermata, Ophiuroidea)

K. Radivojevich-Cross and A. B. Christensen

Current models for climate change predict ocean temperatures will increase by 3.5°C and pH will decrease by 0.2–0.4 units due to increases in CO_2 by 2100. These conditions will greatly affect the metabolism of ectothermic

organisms, like echinoderms. *Hemipholis elongata* and *Amphipholis gracillima* are both burrowing brittle stars often occurring in the same habitat, but having different lifestyles. *H. elongata* does not ventilate its burrow, but relies on oxygen transported via hemoglobin in its water vascular system, while *A. gracillima* ventilates the burrow by arm movements, typical of amphiurid brittle stars. It was hypothesized that these behavioral differences would lead to differences in their responses to climate change variables. Animals were established in burrows and exposed to treatments for a period of 6 wk. Treatments (25°C, 28°C, 32°C; and pH 8.1, 7.8, 7.6) were tested in all combinations; pH 7.8 and 7.6 were achieved by bubbling tanks with CO_2. Oxygen uptake was measured weekly. A repeated-measures design (ANOVA) indicates that there were differences in oxygen uptake between the species ($P = 0.000$). *H. elongata* had lower oxygen uptake across treatments, presumably due to the lack of active burrow ventilation. For *H. elongata* pH ($P = 0.328$) and temperature ($P = 0.563$) had no effect on respiration. For *A. gracillima* temperature had an effect on oxygen uptake, causing a decrease as temperature increased ($P = 0.002$), while pH had no effect ($P = 0.465$). No interaction between pH and temperature was found for either species.

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Sea Cucumbers from the Silurian of the Isle of Gotland, Sweden

M. Reich, M. Kutscher, and T. R. Stegemann

Similar to the situation in other echinoderm groups, the holothurian skeleton disarticulates more or less rapidly after the death of the organism. Fully articulated specimens are consequently known only from a few fossil Lagerstätten deposits, but, however, isolated sea cucumber skeletal elements can be locally abundant. There are only a few reports on Silurian holothurians, but new collections of well-preserved isolated echinoderm material have been made from nearly all Silurian strata of the Isle of Gotland, Sweden. Several hundred marl and rock samples were investigated using micropaleontological techniques. More than 50,000 echinoderm ossicles were isolated in the last 12 yr, including around 1,000 holothurian ossicles. These remains include body wall ossicles of different types as well as more than 500 calcareous ring elements. Based on scanning electron microscopy analysis, the latter ones can be assigned to apodids (Myriotrochidae) and stem group apodids. Others are remarkably intermediate in morphology between members of the Apodida and Aspidochirotida. Surprisingly, a few radial calcareous ring elements show perforations on each lateral (articulating) face, which is (apparently) comparable with a few stem echinoids in which the radial water vessel is fully enclosed within their ambulacral plates. Consequently, they provide new information for the early diversification of the Holothuroidea and the origin of the calcareous ring. The studied holothurian material comes from nearly all Silurian strata of the Isle of Gotland (Landovery: Lower Visby Fm; Wenlock: Upper Visby Fm, Högklint Fm, Slite Group, Halla Fm, Klinteberg Fm; Ludlow: Hemse Group, Eke and Burgsvik Fms). This holothurian material from Gotland is the most diverse sea cucumber fauna ever documented from Silurian strata.

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Modern Holothurian Calcareous Ring Morphology—the Need for More Detailed Studies

M. Reich and P. M. O'Loughlin

The defining feature of all members of the Holothuroidea is the calcareous ring, which is possessed by nearly all modern sea cucumbers. The calcareous ring supports the pharynx, the anterior section of the water vascular system, and provides points of attachment for the longitudinal and (if present) retractor muscles; furthermore, it is known that in some groups, a notch or a perforation in radial elements is present for the passage of radial nerves. However, almost nothing is known about the three-dimensional (3-D) morphology and the stereom structure of the holothurian calcareous ring; similarly, the evolutionary origin of this structure is also uncertain. According to taxonomical studies on modern holothurians, the calcareous ring is considered to be highly important because of major differences in this structure within various orders and families. There are a few reports on fossil calcareous ring elements, but this structure was nearly completely neglected by paleontologists. Isolated fossil calcareous ring elements were mostly misinterpreted as aberrant ossicles or ''fused side shields'' of ophiuroids. However, this structure offers more information, but this can only be deduced through a better 3-D understanding of the calcareous ring of modern sea cucumbers, which is still largely missing. Here we offer

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preliminary results from detailed studies of hard parts using X-ray computed tomography and scanning electron microscopy of members (>15 species) of the Apodida (Chiridotidae, Myriotrochidae), Aspidochirotida (Holothuriidae, Synallactidae), Dactylochirotida (Ypsilothuriidae), Dendrochirotida (Cucumariidae, Psolidae), Elasipoda (Elpidiidae, Laetmogonidae), and Molpadiida (Caudinidae, Eupyrgidae, Molpadiidae).

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A New Elasipodid Holothurian Representative from the Early Devonian Hunsrück Slate Fossil Lagerstätte, Germany

M. Reich and A. B. Smith

Among all five groups of modern Holothuroidea, the elasipodid sea cucumbers are unique in being confined to the deep sea. Nearly 150 species of five families are widely distributed in depths over 200–400 m, and many of them are cosmopolitan in distribution. Modern elasipodids are characteristic of abyssal and hadal depths, where they can be found in deepest trenches, constituting up to 90% of the total biomass. All Elasipodida are strongly bilaterally symmetrical, and they often possess bizarre body forms with elongate projections or transparent veils, whereas the body wall of these forms is fragile and often quite gelatinous. Consequently, the fossil record of elasipodids is very poor and incomplete. All Elasipodida are divided primarily on the basis of their calcareous body wall ossicles and calcareous ring structure. While studying '*Palaeocucumaria*' specimens from the Emsian Hunsrück Slate, we came across two sea cucumbers that were clearly different. These two new specimens are considerably larger than the previously known *Palaeocucumaria* specimens from this fossil Lagerstätte and show no evidence of having the large plated tube-feet that characterize that genus. Furthermore, detailed inspection using X-ray computed tomography of the calcareous ring preserved in situ shows it to be composed of five interradial and radial elements, the latter x-shaped, having typically four processes as in modern deimatid deep-sea holothurians. The new find represents the first unequivocal record of a deep-sea holothurian body fossil from the Paleozoic, and it implies a deep split between Deimatidae and Laetmogonidae (Elasipoda). This indicates that crown group holothurian divergence had taken place by the early Devonian as suggested recently by the authors. The new genus and species is the earliest holothurian body fossil in which there is a clear differentiated sole and ventral mouth—implying this to have been an epifaunal detritus feeder.

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Holothurians from the Carboniferous Mazon Creek Lagerstätte (Illinois, U.S.A.)

M. Reich and T. R. Stegemann

The Mazon Creek biota of northeastern Illinois provides one of the most complete records known of late Paleozoic life. This fossil Lagerstätte is famous for organisms with nonmineralized skeletons. Apart from one single crinoid specimen, the only other echinoderm found is a holothurian, which is actually quite common in the Essex fauna (southern Mazon Creek area). The holothurian was often listed or named as '*Achistrum*,' but this is actually a paragenus name for hooklike ossicles. In contrast to the Braidwood fauna, the Essex fauna represents a brackish and restricted marine habitat, associated with a deltaic environment. After a first mention in the 1950s by Eugene Richardson, these findings were negated over decades. It is surprising that only two preliminary descriptions exist up to now regarding the sparse holothurian fossil record, consisting mostly of disarticulated material. During the last years, we studied more than 3,500 holothurian body fossil specimens. At the present stage of our work, all specimens represent a single chiridotid species of the Taeniogyrinae (Apodida) with a body length of 2–11 cm and a diameter of 0.5–1.5 cm. Well-preserved specimens contain a typical apodid bandlike calcareous ring (diameter 4 mm) of five interradial and five radial elements as well as hook-shaped ossicles of bimodal size (150–250 µm and 550–800 µm), comparable with modern taeniogyrinid sigmoid rods. Almost all ossicles in situ are clearly arranged in rows as in modern forms. Soft-tissue preservation is known from gut traces, but no tentacles have yet been clearly observed. This Mazon Creek species represents the only holothurian body fossil with ossicles and the entire calcareous ring preserved in situ as well as soft-tissue preservation. It also implies a deep split between all apodid families and a very early diversification of this group, as suggested recently by the first author.

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Regenerative Capacity, Biochemical Composition, and Behavior of the Sea Star *Luidia clathrata* Exposed to Near-Future Ocean Acidification Conditions

J. B. Schram, J. B. McClintock, R. A. Angus, and J. M. Lawrence

As atmospheric anthropogenically produced CO_2 is absorbed by oceanic surface waters, the resultant chemical reactions cause a decrease in seawater pH and a shift in carbonate chemistry, generally referred to as ocean acidification, and can have deleterious effects on marine organisms. The majority of research to date has focused on calcified marine invertebrates but the alterations in carbonate chemistry induced by ocean acidification have the potential to affect all marine organisms. This study examines sublethal effects of near-future (year 2100) ocean acidification on the regenerative capacity of *Luidia clathrata*, a key sea star predator in subtropical soft-bottom habitats. The potential impacts of seawater acidification included an examination of arm length regeneration, tissue biochemical composition, and whole animal behavior. Two groups of sea stars, each with two arms excised, were maintained on a formulated diet in seawater bubbled with air alone (pH 8.2) or with a controlled mixture of air/CO_2 (pH 7.8). Arm length, total wet mass, and righting responses were measured regularly. At the completion of the experiment (14 wk), pyloric cecal indices, soluble and insoluble protein, soluble carbohydrate, lipid, and ash (inorganic content) were determined for arm body wall and pyloric cecal tissues to assess quantity and quality of regenerated and intact tissues. Despite a slightly shorter regenerated arm length, the present study indicates that predicted near-term levels of ocean acidification (seawater pH 7.8) do not significantly alter arm regeneration rates, biochemical composition, or behavior in *Luidia clathrata*.

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Ocean Acidification and Sea Urchin Fertilization: A Cautionary Tale with the Antarctic Sea Urchin *Sterechinus neumayeri*

M. A. Sewell, P. Yu, L. Kapsenberg, and G. E. Hofmann

Fertilization is the foundation stage of development in marine species; therefore any change to environmental conditions that negatively affects fertilization success has the potential to profoundly affect population recruitment and persistence. Ocean acidification (OA), a reduction in ocean pH due to the uptake of anthropogenic carbon dioxide (CO_2) by surface waters, is a potential environmental stressor for fertilization and has recently been the focus of study in many marine invertebrates. Studies of echinoderm fertilization in OA conditions using species from temperate and polar environments have, however, produced variable results, ranging from highly negative effects of OA to no effect except at pHs greater than those predicted for the next 300 yr. In experiments conducted on the Antarctic sea urchin *Sterechinus neumayeri*, we found that the effect of OA was negative in 71% of the trials with single male–female pairs (5/7) at a pH of 7.8, a result in contrast to the previously published results for this species, where there was no effect of pH on fertilization success until pH < 7.3. In this talk we will discuss the importance of gamete source (single male–female vs pooled gametes), statistical issues, and the lessons that we should be taking from ecotoxicology in the standardization of OA fertilization experiments.

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Habitat Selection and Ecology of Brittle Stars on Deep-Sea Corals

T. C. Shirley, K. A. Lavelle, and P. J. Etnoyer

Two species of euryalid brittle stars, *Asteroschema laeve* and *A. tenue*, were among the most common and conspicuous macrofauna on octocorals from 300- to 700-m depths off Roatan, Honduras. A third euryalid, *Asteroporpa annulata*, occurred on a similar but unidentified octocoral in much shallower depths, <300 m.

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Transects were conducted vertically from 700- to 100-m depths in 10 dives with a three-person submersible on two separate expeditions in 2010 and 2011; high-definition video, digital photography, and oceanographic measurements (CTDO) were recorded. The two congeneric brittle stars comprised 22% of all macrofauna observed on 24 species of deep-sea corals, but differed greatly in their habitat. *Asteroschema laeve* occurred only on yellow and purple *Parmuricea* spp. octocorals, while *A. tenue* was observed only on *Antipathes* sp.; both coral species were sympatric and within the same depth range. The two brittle-star species never co-occurred and were primarily on larger specimens of the octocorals, and not on the many other coral species. The number of brittle stars varied with the size of the octocoral; small *Paramuricea* would host a single brittle star, while larger *Paramuricea* could have >20 specimens of these large brittle stars. Both congeners shared their coral hosts with other macrofauna, including crinoids, the brisingid sea star *Novodinia antillensis*, galatheoid crabs (*Eumunida picta* and *Chriostylus* sp.), and numerous unidentified juvenile crabs. Juveniles of both brittle-star species were rarely observed. Most individuals of *Asteroschema* spp. had characteristic regenerating arm tips, displaying evidence of predation, but no predator was identified. Photographs of the same octocoral individual taken 2 yr apart show what appears to be the same brittle star.

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A Perplexing Genus *Cassidulus* Lamarck (1801): What Is in It?

C. Souto, L. Martins, and C. Menegola

Since its description, *Cassidulus* Lamarck presents many problems concerning the validity of its name (since it was supposedly preoccupied among Mollusca), type-species (not clearly defined by Lamarck), and a great list of synonyms considered by some authors (e.g., *Pygorhynchus, Procassidulus, Rhyncholampas*). Indeed, the latter led Mortensen to consider *Cassidulus* the most perplexing cassiduloid genus. Moreover, *Cassidulus* has been the trash can of the cassidulids and little is known about its species. To verify and list the valid *Cassidulus* species 120 papers/books on cassidulid taxonomy from 1801 to 2010 were analyzed, revealing that about 106 species were described in this genus. From these, only 10 are recognized as a valid *Cassidulus* species (*C. caribaearum, C. californicus, C. ellipticus, C. ynezensis, C. infidus, C. mitis, C. senni, C. mestieri, C. kieri*, C. *santolayae*), 56 were assigned to other genera (mostly *Rhyncholampas* and *Hardouinia*) or synonymized, and 40 remain with an unknown taxonomic status. Besides the 10 mentioned species, 3 others, originally assigned to other genera, should join the list: *C. peruvianus, C. falconensis*, and *C. malayanus*. Apparently, all recent species are well established and the questions rely mainly within the fossils, probably as a consequence of poor descriptions (especially because of the specimens' integrity), the inaccuracy of species drawings (since some characteristics were not considered as important as they should), and the inaccessibility to relevant bibliography. Furthermore, its taxonomy is poorly studied and *Cassidulus* species have been confounded to *Rhyncholampas* and *Eurhodia*. With many intermediate forms among them, limiting these genera has not been easy. This search revealed that there still remains much work to be done on the alpha taxonomy of the cassidulids before any robust phylogenetic and biogeographic analysis can be done. Therefore, this search will continue aiming to assess the documented history and list all valid species of *Cassidulus*.

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Down-and-Dirty: What Holothurians and Hoover Vacuums Have in Common in a Tropical Coral Reef Environment

A. Tan, E. Manley, and J. Nestler

Nearshore reefs are experiencing increased sedimentation from human land use practices and altered precipitation resulting from global climate change, presenting a major threat to the sustainability of coral reef systems. Some coral species can remove moderate amounts of sediment using mucus and cilia; however, high sediment loads increase the probability of coral bleaching and death. The purpose of this research was to examine the extent to which sea cucumbers remove sediment from coral. A 2,000-m^2 research area in the southern Philippines consisted of 12.8% live coral, 5.2% dead coral, 26.8% coral rubble, and 32.7% sand. Sea cucumbers (*Pearsonothuria graeffei*) were preferentially found on live coral (38.2%), whereas they were less likely to be found on dead coral (0.4%) or sand (5.5%; G-test, $P < 0.001$). Live coral on which *P. graeffei* were located had a sediment mass of 18.4 $\pm$ 3.3 mg/cm^2 before the passage of a sea cucumber over the area, and a sediment mass of 6.8 $\pm$ 1.8 mg/cm^2 immediately after

passage of a sea cucumber over the area (n = 28; t-test, $P < 0.001$). *P. graeffei* removed 63.0% of sediment from live coral (11.6 mg/cm^2). Sediment accumulation rates in the research area were 2.4 ± 0.5 mg/cm^2 d^{-1} (n = 15); thus an individual *P. graeffei* was able to remove about 5 days' worth of sediment accumulation each time it passed over an area of live coral. A model was constructed by conducting a census of *P. graeffei* in the entire area and determining the area of live coral each could pass over in a given time period. This model suggests that all live coral in the research area could be ''vacuumed'' by a sea cucumber 15 times in a year.

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Toward a Hierarchy of Controls on Crinoid Preservation: Taphonomic Variability at Low Taxonomic Levels and the Relative Influence of Environmental, Ecological, and Morphological Factors

J. R. Thomka

Crinoid fossil and subfossil preservation is controlled by an impressive number of variables. These can be classified into three slightly overlapping categories: (1) environmental factors, including background sedimentation rate, frequency and magnitude of rapid burial events, water temperature, sediment grain size, and benthic oxygenation; (2) ecological factors, including scavenger preferences, presence of commensal or parasitic organisms, and depth and intensity of bioturbation; and (3) morphological factors, including specimen size, composition of connective tissue, and cup flexibility. Yet, despite recognition of these diverse taphonomic influences, the relative significance of each factor remains undetermined; that is, a hierarchy of controls on crinoid preservation has not yet been identified. Assessment of taphonomic variability at refined taxonomic levels within individual subclasses and orders shows promise for revealing taphonomic patterns, particularly those overlooked by studies focusing on comparisons between depositional facies or between significantly different crinoid morphotypes. Intergeneric, interspecific, and intraspecific taphonomic patterns, drawn primarily from detailed case studies of Middle Silurian and Upper Pennsylvanian North American crinoids, indicate that environmental factors are most significant, as these tend to control the biotic composition of facies, and therefore, the associated crinoid assemblage and paleoecological dynamics. Further, it appears that a more precise hierarchy of taphonomic influences, incorporating specific variables within each of the three aforementioned categories, can be developed for individual crinoidal deposits. Future comparative taphonomic research may lead to the development of a comprehensive hierarchical model that addresses the myriad of crinoid-bearing depositional environments.

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New Ophiacanthid Brittle Stars from the Late Triassic of Japan: Shallow-Water Origin of an Extant Deep-Sea Group?

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Many modern deep-sea groups constituted an abundant and diverse component of shallow-water communities in Mesozoic times. Well-known examples among echinoderms are stalked crinoids and leather sea urchins. Some of these groups were even first known as shallow-water fossils before extant representatives were discovered in the course of deep-sea exploration. These differences in bathymetric distribution imply significant shifts in habitat preferences over time, and raise the question as to whether modern deep-sea groups originated in shallow-water settings and subsequently migrated to deeper habitats, or whether the shallow-water representatives are temporary invaders from a primarily deep-sea lineage. Here, we report on brittle-star fossils from the Carnian (early Late Triassic) of Yamaguchi, Japan, which are unequivocally assignable to the Ophiacanthidae, an extant brittle-star family almost exclusively found in deep-sea settings but also displaying a diverse late Mesozoic shallow-water record. The material was found in shales interpreted as shallow-marine deposits intercalated between terrestrial to marginally marine strata. Besides being by far the oldest known members of the Ophiacanthidae, the Japanese specimens display a combination of characters that places them close to the base of the Ophiacanthidae, thus corroborating a shallow-water origin of the family. A preliminary cladistic analysis, however, does not support a basalmost position of the Japanese specimens within the Ophiacanthidae, suggesting the existence of even more basal ophiacanthid lineages, the fossil evidence of which remains to be discovered. At the present state, especially with the almost inexistent knowledge on the fossil record of early Mesozoic deep-sea benthos, it is not possible to definitely constrain the origin of the Ophiacanthidae.

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Modern-Type Coral-Associated Brittle-Star Fauna in the Middle Miocene of Central Europe

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Echinoderms are a key component of coral-reef invertebrate communities, and although brittle stars are probably among the least conspicuous representatives of this group, they are highly abundant and diverse in modern coral reefs. Here, we report a brittle-star assemblage from the middle Miocene of Austria. The assemblage consists of numerous dislocated skeletal plates, including the highly diagnostic spine-bearing lateral arm plates, retrieved from sediment infillings within a coral patch reef of the Central Paratethys. Preservation of the plates is such that a detailed comparison with the corresponding plates of modern relatives is possible. The middle Miocene assemblage is strikingly similar to modern coral-reef brittle-star communities on family level, and in most cases even on genus level. Almost all of the groups typically found in present-day coral-associated brittle-star communities could be unequivocally identified in the Miocene assemblage. Remarkably, even the relative abundances of the groups in the Miocene fauna are comparable with those found in modern equivalent communities. These observations imply that coral-associated brittle-star communities have remained largely unchanged since the last 15 Ma. In the light of recent hypotheses conferring a leading role to coral reefs in producing evolutionary innovation, the conservatism of brittle-star communities is puzzling and suggests that the mechanisms favoring high origination rates affect individual groups in different ways.

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The Contribution of John Holmes Dearborn to Polar and Echinoderm Biology

R. L. Turner

The scientific record of the career of John Holmes Dearborn (1933–2010) began in 1955 when he graduated from the University of New Hampshire with a B.A. in zoology and with the polychaetous patronym *Harmothoe dearborni* Pettibone, 1955. An M.S., a Ph.D., a mollusk, a fish, and a mountain followed over the next dozen years. Dearborn was among the earliest American biologists in what G. A. Knox dubbed the ''modern era of Antarctic biological investigations,'' begun in 1958 with IGY and Dearborn's first stay at McMurdo Station. His dissertation research formed the groundwork for Knox's ''new breed of Antarctic biologist.'' Dearborn's early interest in cold-water marine life was broad: after 12 yr of publications about crustaceans, fish, birds, mammals, and general faunistic polar studies, it was not until 1969 that his first work solely on echinoderms appeared, on distribution of Antarctic crinoids, coauthored with Janis Rommel. The remaining 30 yr of his career were focused on polar asteroids and ophiuroids, particularly their feeding ecology. Dearborn led the way with his studies on *Labidiaster*, *Ophionotus*, *Astrotoma*, and other friends. His papers on feeding ecology have enjoyed very steady citation rates in the last three decades. In addition to rather thick ice, the platforms for his research on benthic ecology in the Antarctic and Arctic included several oceanographic research ships and submersibles. Only through the research of a very few of his graduate students did Dearborn vicariously experience the tropics; but where would the tropics be were it not for the poles? Dearborn's list of patronyms ended in his retirement with a pond in Maine, the state of his birth and death.

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Reproductive Cycle of Sand Dollar, *Peronella lesueuri,* in Cockburn Sound, Western Australia

S. Yeo

Using histological methods, the reproductive cycle of *Peronella lesueuri* in Cockburn Sound, Western Australia was studied to determine the periodicity as well as the degree of gametogenic synchrony. The gametogenic cycle consists of three main phases: growth—when gonads accumulate nutritive material for gametogenesis; maturation—when gametogenesis and spawning occur; and spent—when nutritive phagocytes reabsorb relict

gametes and gonads are either devoid of gametes or only contain relict gametes or gametocytes. Data from the first year of a 2-yr study is being presented. From histological photographs, five gametogenic stages have been identified in both sexes, although stages were not distinct in all cases. Males were classed into stages qualitatively and females were staged according to the proportions of oocyte classes within the gonads. The data suggest an annual reproductive cycle with spawning taking place during late summer and autumn. The data also indicate that both sexes are in gametogenic synchrony with spent stage occurring from June to October (winter–spring).

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Molecular Anatomy of the Regenerating Digestive Tube in the Sea Cucumber *Holothuria glaberrima* (Echinodermata: Holothuroidea)

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In recent years, a large amount of information has been obtained on cellular mechanisms involved in visceral regeneration in holothurians, including cell death, cell division kinetics, and phenotypical changes accompanying dedifferentiation and redifferentiation. In addition, modern techniques of high-throughput transcriptome analysis have yielded sets of genes that are differentially up-regulated or downregulated at certain stages of regeneration. However, complete understanding of regeneration is impossible without establishing a connection between these two pools of data; that is, determining the nature of the cells expressing a particular gene at a particular time point. In the present study, we employ nonradioactive in situ hybridization techniques, which combine good tissue morphology preservation with high sensitivity of transcript detection to map gene expression in the regenerating digestive tube. We investigated localization of transcripts of *Bmp-1*, *mortalin*, *survivin*, *TCTP*, and *Wnt9*, the genes that have been previously known to be implicated in embryogenesis or cancer. The choice was determined by our long-term goal of trying to understand how the developmental regulatory pathways known to be involved in tumor development can be activated in posttraumatic regeneration without leading to malignant growth. The gene expression data combined with the available morphological information highlight the gut mesothelium (the outer layer of the digestive tube) as a highly dynamic tissue whose cells undergo remarkable changes in gene expression in response to injury. These changes coincide with drastic dedifferentiation events and a burst of cell division and apoptosis.

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